ORTHOGENETIC EVOLUTION OF DEGREE OF DIVERGENCE BETWEEN CARPEL AND FOLIAGE LEAF.

STUDIES IN DETERMINATE EVOLUTION. VI*.

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In the fourth paper of the present series on the nature of the evolutionary process, a brief presentation was given of the progressive divergence of character between the sporophyll and foliage leaf as one follows up the evolutionary sequence from the homosporous pteridophytes to the angiosperms.† A general series of sporophylls is now presented in order to illustrate the principle of progression and degree of divergence in detail. Only a carpellate series is given as the carpel is usually somewhat slower in attaining the extreme limits than the stamen. However, the stamen shows the same general sequence also, often in a very striking manner.

In the lower fern series, both eusporangiate and leptosporangiate, there is no difference whatever between the foliage leaf and the sporophyll except that the latter develops sporangia. In other words, the sporophyll is a foliage leaf and has all of its functions. These lower vascular plants are extremely simple systems as compared with the highest angiosperms. Figure 1 represents a leaf of Goldie's Shield-fern, *Dryopteris goldiana* (Hook.) Gr. The upper part of this specimen has sporangia while the lower part is sterile with the characters of the completely sterile foliage leaf. In this species, as in most of the lower ferns, some leaves are sterile, some are partly sterile and partly fertile, and some have the entire lamina covered with sori. There is, however, no dimorphism of any kind except that the reproductive areas have sori.

The first distinct step in the orthogenetic sequence is shown in a difference in size between foliage leaf and sporophyll.

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†Long-continued Determinate Orthogenetic Series. Ohio Jour. Sci. 31: 1–16. 1931.

This is well represented by *Asplenium pycnocarpon* Spreng., the Narrow-leaf Spleenwort (Fig. 2, a and b). The leaflets of the Sporophyll are usually smaller and considerably narrower than those of the sterile foliage leaves. There is thus the beginning of a degree of divergence between the two homologous organs. The leaves of the Net-veined Chain-fern,

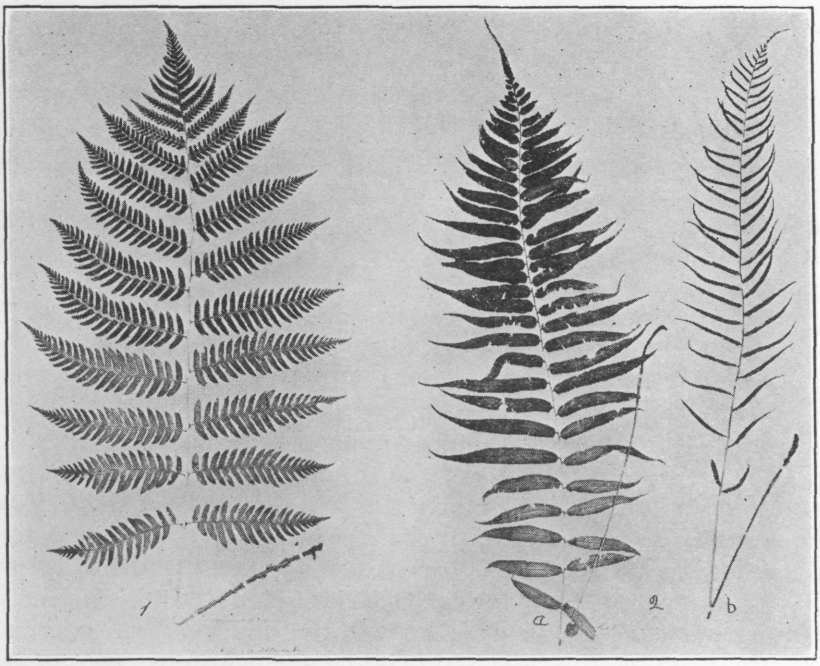

FIG. 1. *Dryopteris goldiana* (Hook.) Gr. A sporophyll with the lower pinnae sterile.
FIG. 2. a—Foliage leaf of *Asplenium pycnocarpon* Spreng.
b—Sporophyll of the same.
(All reduced to one-sixth natural size.)

Lorinseria areolata (L.) Presl. (Fig. 3, a and b) are more decidedly dimorphic, the pinnae of the sporophylls being greatly reduced in width. The extreme divergence in our native fern series is attained in the Sensitive-fern, *Onoclea sensibilis* L. (Fig. 4, a and b). The sporophyll is remarkably different from the foliage leaf. The foliage leaf is broadly triangular, deeply pinnatified, and with the segments usually undulate, sinnate dentate, or somewhat pinnatifid, while the sporophyll is without any expanded blade and is bipinnate. The pinnules

are contracted and inrolled over the sori into round, hard, bead-like bodies which become brown when mature. Several important hereditary potentialities have been added to the protoplast which come into action when the physiological gradient of the system, at the given point, is of such a nature as to throw the leaf into the reproductive activity. The

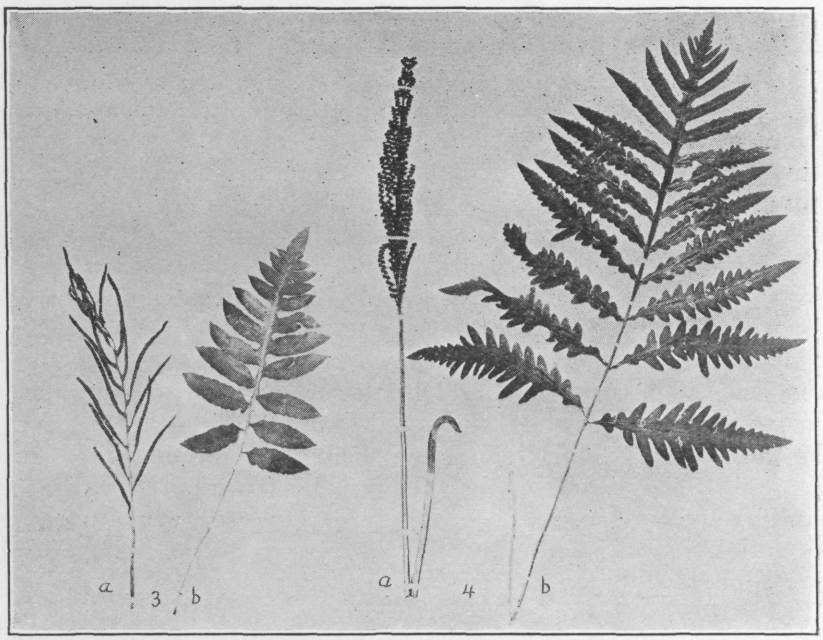

FIG. 3. a—Sporophyll of *Lorinseria areolata* (L.) Presl.
b—Foliage leaf of the same.
FIG. 4. a—Sporophyll of *Onoclea sensibilis* L.
b—Foliage leaf of the same.
(All reduced to one-sixth natural size.)

divergence of the sporophyll from the foliage leaf is shown most prominently by the compound condition of its pinnae, by the change in texture of the contracted leaf blade tissue, by the great reduction in the size of the pinnules, and by the inrolling of the pinnules over the sori. All these and other differences show a culmulative addition of potentialities in the protoplast. The same evolutionary sequence is shown in other families of living ferns.

There are only a few living heterosporous pteridophytes and none whatever that might form a transition link between the ferns and the lowest living seed plants, the cycads, the living heterosporous ferns all being extremely specialized and reduced plants. The orthogenetic sequence is, however, consistently continued in the lowest living Cycadales. In passing up to the cycads, a number of very fundamental potentialities have been added to the cell complex, which show their presence in the sporophylls. The time of sex determination has been shifted from the gametophyte to the sporophyte in the life cycle, and in all seed plants this determination always takes place at least as early as the beginning of the development of the sporophylls. The sporophylls, therefore, normally always show secondary sex dimorphism, while in the fern series there is no sex expression whatever, the entire sporophyte, including the leaves, being in the neutral state. The difference in sexual state, therefore, gives microsporophylls or stamens and megasporophylls or carpels. Because of the presence of the secondary female state in all the cells of the carpel, the carpel will produce megasporangia or ovules and in these megaspores. Since the megaspores are not shed, the female gametophytes are parasitic in the ovules. Thus many new hereditary potentialities are present to be expressed in the carpel as compared with the simpler system in the sporophyll of *Onoclea*, while nothing essentially new is added to be expressed in the foliage leaf except a few minor characters.

The lowest living cycad is *Cycas revoluta* Thunb. Figure 5 represents a carpel of this species. The carpellate leaf is greatly reduced in size when compared with the large pinnately compound foliage leaf. The blade of the carpel is still present showing prominent pinnules. The texture, surface, and color are decidedly different from the foliage leaf. The general differences are the same as in *Onoclea* but there is no tendency to enclose the sporangia in the leaf blade.

Figure 5 represents a carpel of *Cycas circinalis* L., which shows a considerable reduction in the leaf blade when compared with *Cycas revoluta*. An extreme type of *Cycas* carpel is represented by *Cycas normanbyana* F. Muell. (Fig. 7). In this species the ovules are reduced to two and the compounding of the vestigial blade is practically obliterated. There is therefore a decided difference between the carpel and the large, green, pinnate foliage leaf.

All the sporophylls considered so far are produced on indeterminate axes. The remaining members of the series are all flowering plants, the carpels being produced on definitely

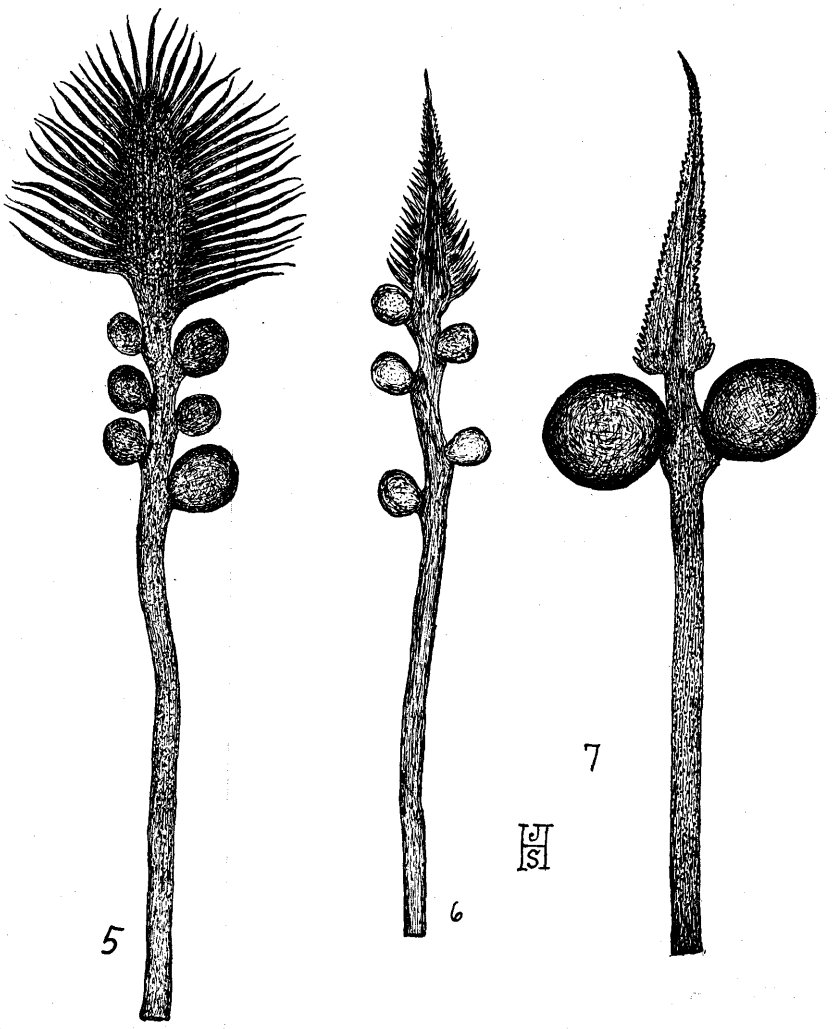

FIG. 5. Carpel of *Cycas revoluta* Thunb.
FIG. 6. Carpel of *Cycas circinalis* L.
FIG. 7. Carpel of *Cycas normanbyana* F. Muell.
(All reduced to one-half natural size.)

determinate reproductive axes. It will be seen that the reduction of the sporophyll in the evolutionary progression is not dependent on the introduction of a determinate reproductive

bud. The progressive reduction and specializiation of the sporophyll is an entirely independent evolutionary movement, although, of course, in all the higher forms the orthogenetic evolution of the carpel is necessarily associated with the orthogenetic evolution of determinateness of the floral axis.

Figure 8 represents a carpel of *Macrozamia fraseri* Miq. A decided reduction has taken place in the carpel as a whole when compared with the *Cycas* series. The petiole is very short although the petiole of the foliage leaf is comparable to those in *Cycas*. The ovules have changed their position and this new character is continued through the rest of the living cycad series. The last vestige of compounding has disappeared from the carpellate blade. In *Macrozamia denisoni* Moore and F. Muell. (Fig. 9) the carpellate blade is again much shorter than in the preceding species. The extreme is reached in species of *Zamia*. Figure 10 represents a carpel of *Zamia ulei* Dammer in which the blade is represented by a mere peltate cap and the entire structure is more contracted and compact. In *Ginkgo biloba* L. a much higher type of the Cycadophyta, where again there is no floral development, the blade of the carpel is reduced to a minute, transverse vestigial ridge, although the petiole is as prominent as the petiole of the foliage leaf.

The next higher group in the upward progression is the class of the Coniferae and the lowest plants in this series are the Araucariales, as indicated by their simple, rhythmical ontogenetic gradients, their primitive leaf arrangements, lack of peduncles, frequent proliferation of cones, and multicellular male gametophytes. In *Araucaria araucana* (Mol.) Koch. (*A. imbricata* Pav.), the carpel has a green leaf blade of considerable size (Fig. 11) while in *Araucaria rulei* F. Muell. the blade is decidedly reduced (Fig. 12). In *Cunninghamia sinensis* R. Br. (Fig. 13) the lowest living member of the Pinnales, although the carpel still shows a distinct midrib, it is much smaller and decidedly different in character from the foliage leaf. In the Pinaceae, the carpellate bract (blade) shows a progressive reduction in the various phyletic lines, although the problem is complicated by the evolution of a new structure, the ovuliferous scale, which makes the degree of divergence between the carpel and foliage leaf (needle leaf) unusually large. The extreme in specialization in the Pinales is reached in *Juniperus*. Figure 14 represents a carpel of *Juniperus*

virginiana L., the Red Juniper, magnified two diameters. These carpels are decidedly different in texture from the foliage leaves although nearly comparable in size. After pollination, the carpels of the minute cones all fuse together, become fleshy, and are of a dark blue color, so that the mature fruit finally simulates a juicy berry instead of a strobilus, which it is structurally. Thus the divergence between carpel and foliage leaf has been increased by the addition of important

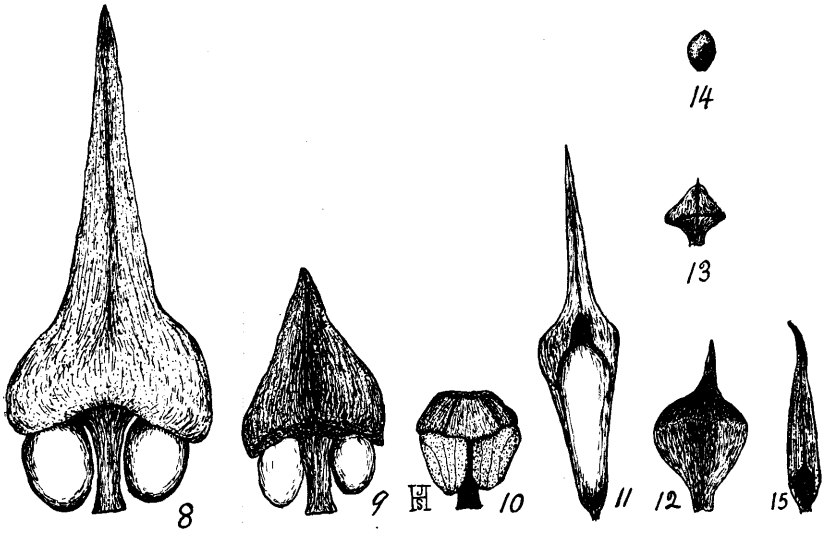

FIG. 8. Carpel of *Macrozamia fraseri* Miq.
Fig. 9. Carpel of *Macrozamia denisoni* Moore & F. Muell.
FIG. 10. Carpel of *Zamia ulei* Dammer.
FIG. 11. Carpel of *Araucaria araucana* (Mol.) Koch.
FIG. 12. Carpel of *Araucaria rulei* F. Muell.
FIG. 13. Carpel of *Cunninghamia sinensis* R. Br.
FIG. 14. Carpel of *Juniperus virginiana* L.
FIG. 15. Carpel of *Magnolia pterocarpa* Roxb.

(All reduced to one-half natural size except Fig. 14, which is magnified two diameters.)

characteristics to the former, which parallel more or less similar advances in the carpels of great numbers of angiosperm series. At the top of the next higher conifer series, the Taxales, the reduction of the carpellate strobilus and the carpel have reached the ultimate limit in *Taxus canadensis* Marsh. The whole structure is represented by a single ovule on a cushion of tissue from which a fleshy red aril develops after fertilization, and beneath this is an involucre of specialized leaf bracts.

The Angiospermae are an exceedingly complex group with many progressive phylogenetic series in both the Monocotylae and Dicotylae. In general the orthogenetic progression is essentially the same in all of them. The main series from the bottom to the top is represented by figures 15 to 23. The lowest type of known angiosperm carpel, as Hutchinson* has pointed out, is found in *Magnolia pterocarpa* Roxb., from the Himalaya region. Figure 15 represents a carpel of this species reduced to one-half the natural size to correspond with the preceding conifer series beginning with *Araucaria araucana* (Mol.) Koch. (Fig. 11). In order to represent the angiosperm series properly the carpels have been magnified two diameters. *Magnolia pterocarpa* is repeated in figure 16 so that a direct comparison can be made with the rest of the angiosperms. It will be noted that this carpel is very leaf-like, being flat and showing a sort of midrib and a comparatively inconspicuous stigma at the tip. *Liriodendron tulipifera* L. also has a thin flat carpel (Fig. 17). Passing upwards to flowers with a single cycle of carpels, a further advance has taken place as shown by the more typical apocarpous carpel of *Aquilegia canadensis* L. Figure 19 shows a somewhat more advanced type of carpel from the monocotyl series, in the loosely syncorpous condition of *Yucca filamentosa* L. A similar loosely syncarpous condition is also present in the dicotyledonous *Abutilon abutilon* (L.) Rusby, in which the leaf character of the carpel is still slightly in evidence (Fig. 20). Figure 21 represents a carpel from the specialized syncarpous gynecium of *Asclepias incarnata* L. The leaf character is becoming very obscure because of the complication of hereditary factors which are thrown into activity at this point in the ontogenetic differentiation. The degree of divergence from the character of the foliage leaf of the species is, therefore, very great. In the next step, the final general limit of the possible evolutionary progression is attained in the development of epigyny. Figure 22, a and b, represent long-style and short-style carpels of the dimorphic *Houstonia coerulea* L. Here the real carpel is represented merely by the top of the ovulary, the style, and the stigma. The lower part of the ovulary, represented below the dotted lines, is cauline tissue which was developed and differentiated

*HUTCHINSON, J. The Phylogeny of Flowering Plants. Proc. International Cong. Plant Sci. Ithaca, N. Y. *1:* 413-421. 1929.

from the cortical rim around the center of the bud after the bud had stopped its growth in length.

The extreme limit of carpel specialization and divergence from the foliage leaf type is reached at the tips of the various

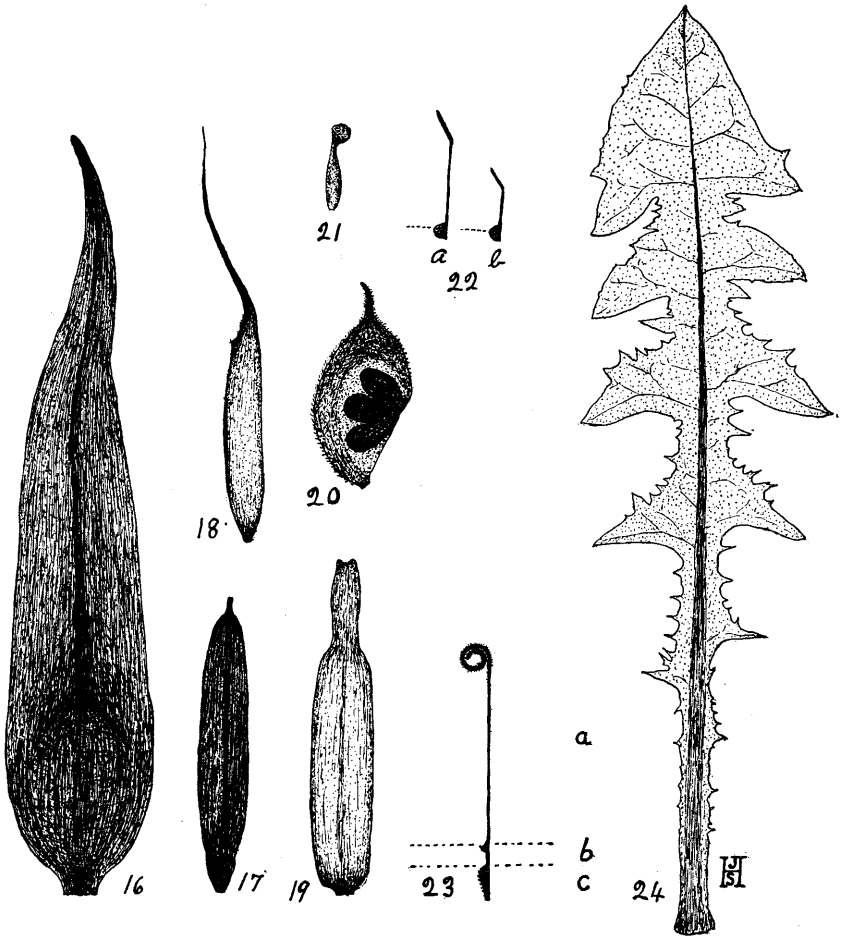

FIG. 16. Carpel of *Magnolia pterocarpa* Roxb.
FIG. 17. Carpel of *Liriodendron tulipifera* L.
FIG. 18. Carpel of *Aquilegia canadensis* L.
FIG. 19. Carpel of *Yucca filamentosa* L.
FIG. 20. Carpel of *Abutilon abutilon* (L.) Rusby.
FIG. 21. Carpel of *Asclepias incarnata* L.
FIG. 22. a and b—Long style and short style carpels respectively of *Houstonia coerula* L.
FIG. 23. Carpel of *Leontodon taraxacum* L.
FIG. 24. Leaf of *Leontodon taraxacum*.

(All magnified two diameters except Fig. 24, which is one-half natural size.)

advanced phylogenetic lines of the higher angiosperms. Figure 23 represents a carpel of the Common Dandelion, *Leontodon taraxacum* L. This represents the very extreme culmination of the angiosperm evolutionary series. The real carpel is again represented morphologically only by the slender style and the coiled stigma (The portion *a*). All the ovulary except the cap over its unilocular cavity represents cortical tissue surrounding the center of the determinate flower bud, the ovulary factors and ovules not being expressed in the actual tissue representing the vestigial carpellate leaf. The ovulary itself shows an extreme specialization, being differentiated into two definite regions, the lower part of the cavity containing the single ovule and the upper part, just below the rim of tissue originally supporting the pappus and corolla tube, developing into a long slender neck. This neck is the structure which at the maturity of the seed elongates greatly to form the slender stem or thread connecting the fruit below with the pappus parachute above. Figure 24 represents an average leaf of the Dandelion reduced to one half natural size while the carpel in figure 23 is magnified to twice its natural size. A comparison of the two structures, which are homologous organs, will show the enormous divergence in form and function which has evolved. The measure of this degree of divergence is a measure of the position of the plant in the evolutionary scale. Almost as great a divergence of character is discovered if one compares the cross section of the stem bearing the leaf rosette with that of the pedicel below the individual florets. In this case also, the extreme of evolutionary complexity is again revealed when one compares the cross sections with each other of the rosette-bearing stem, the scape, the disk, the pedicel, and the lower part of the ovulary, which, as stated above, also represents cauline tissue. Such comparisons show the enormous complexities of the hereditary potentialities of the cell of the Dandelion when compared with that of a fern like *Dryopteris goldiana*, where the cell has the potentialities to produce but one kind of stem and one kind of leaf.

In the evolution of the carpel, then, there is an orthogenetic series progressing ever in one direction from the lowest to the highest types of vascular plants and the same progression is carried out in essentially the same way in all the multitudinous ramifications of the phylogenetic tree. The spectacle is truly marvelous and is not amenable to any anarchistic or witch-

doctor explanations of evolution, such as are still commonly given out at the present time. The evolution of the carpel is found to be strictly *kinetic*, *intrinsic*, *orthogenetic*, *progressive*, in a general sense *irreversible*, and *determinative*. It proceeds by the addition, step by step to the hereditary constitution of the cell, of fundamental potentialities which are neither initiated nor given direction by any apparent condition of the environment nor by any process of environmental selection. Those who still cling to teleological explanations like Lamarekian use and disuse, Darwinian natural selection, response to environment, or the newer deductions from experimental changes induced by x-rays or by other types of radiation, merely show their ignorance of the taxonomic system and the nature of the processes that were necessary to bring it into existence. The mutations brought about by chromosome aberrations or by the injury resulting from the effect of natural or experimentally produced radiation are not of the category one encounters in a study of the evolution of organisms. Neither the artificially induced mutations nor the abundant minute, natural mutations, which are purely superficial phenomena, give any evidence at present as to the nature of the processes which brought about the great fundamental, segregative, persistent changes, responsible for phyla, classes, orders, etc. nor for the remarkable orthogenetic movements, one of which is outlined in the present paper, which kept their steady course through great numbers of types of morphological systems and all sorts of environmental conditions. We must not confuse the problem of minute variation around a center and the problem of speciation with the real building up process of the fundamental potentialities which apparently never undergo change, never are entirely lost, never reversed when once fully established in the protoplast. Inhibitors or modifiers may be developed in the protoplast, or the environment may cause an ontogenetic change in the usual expression, but apparently not a real loss of any fundamental potentiality. The taxonomic system, which after all is what any theory of evolution is supposed to attempt to explain, is a direct contradiction of the belief that fundamental potentialities are subject to the same instability as one finds for the ordinary unit factors or genes with which Mendelian heredity is concerned.

Many of the present pronouncements on evolution would cause one to think that their authors had never indulged in a

study of the appearance and sequence of organisms in relation to geological time, had never made any study of the general taxonomic systems of plants or animals, but seemed to think that all one needed to concern himself about was an endless number of species and varieties which had no more fundamental relationships to each other than the pebbles on a beach and could be changed in one direction or another just as one can change the pebbles by use of hammer or file.

A Program for Teaching Science.

Anyone interested in the teaching of any of the sciences should read this yearbook which deals exclusively with a program for science teaching beginning on the elementary level and continuing through the secondary to the college level. It deals with many phases of the question from content and objectives to the training of science teachers in college. While one may disagree with some of the details given in the plan, it represents much thought and study on the subject and one must agree that it offers unity and continuity in the form of a definite program for science instruction instead of a few scattered and often unrelated courses in scientific subjects, a condition which is so much in evidence in our public schools today—D. F. MILLER.

The committee responsible for the thirty-first edition of the YEARBOOK (Part I) consisted of: Gerald S. Craig, Elliot R. Downing, Charles J. Pieper, Ralph K. Watkins, Francis D. Curtis and S. Ralph Powers (Chairman). The editor is G. M. Whipple.

The Thirty-first Yearbook of the National Society for the Study of Education; Part I; "A Program for Teaching Science," Public School Publishing Co., Bloomington, Ill., 1932. xii + 370 pp. Paper, $1.75; Cloth, $2.50.

Plants and Their Actions.

This pleasing little book was written according to the author so that the layman interested in fundamentals of science could "obtain some knowledge of Natural Science . . . . not primarily as a preparation for examinations." This is admirably accomplished. In simple non-technical language Professor Seward explains some of the major aspects of plants and how they act. Among other things he brings out in startling clearness the "Superiority of Green Plants to Animals" and our great debt to the plant group as a whole.

The entire book is extremely well written and although a glossary of 40 terms is included, there is little need for it, as each term as it appears is well explained.

A list of 17 texts and Floras are appended; these are, as would be expected, primarily British.—W. BERRY.

Plants: What They Are and What They Do, by A. C. Seward. 12 mo., 141 pp., 31 text-figures, Glossary and Index. New York, The Macmillan Co. $1.50.

Darwin's Bulldog.

This book makes a welcome addition to the existing biographies of Huxley. Like Huxley's own life, it is dynamic and vital, carrying the reader along on a continuous wave of action. Huxley liked to call himself Darwin's Bulldog, feeling that his mission was to defend evolution against all attacks. The author of the present volume goes farther, and credits Huxley with the creation of the evolutionary concept as it stands today—namely, the concept of man's natural place in the evolutionary sequence, and the implications arising from such a concept. The book provides fascinating and even exciting reading, and should be read by everyone interested in life and life processes—and who is not?

Huxley, by Clarence Ayers. 254 pp. New York, W. W. Norton & Co., 1932. $3.00.